Pattern selection in models of ocular dominance column development

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Abstract

Several mathematical models have been proposed to explain the developmental origin of ocular dominance columns in the primary visual cortex. The qualitative character of the two dimensional patterns formed by these models is similar, for reasons which have not been previously investigated. In this paper, it is shown that the two dimensional pattern selection properties of a model depend primarily on the form of the nonlinearities in the model. Nonlinear mode amplitude equations are derived for a simplified ocular dominance model using existing techniques from the physics of spatially extended media. The simplified model, which consists of a single nonlinear integrodifferential equation, is shown by computation to capture the essential pattern-forming capabilities of more complicated models. Solution and stability analysis of the amplitude equations yield criteria by which it may be determined which particular two dimen-

sional patterns will form, given a set of model parameters. These results lead to new insight into the properties of existing models and the functioning of the biological system.

Introduction

Sensory input to the cerebral cortex is in many cases organized into spatial maps of particular features of stimuli. Examples from the primate visual system are the maps of retinotopy, orientation selectivity, and ocularity. This paper is concerned exclusively with the spatial maps of ocular dominance, or eye-preference, by cells in the primary visual cortex. The anatomical correlates of ocular dominance columns, spatially varying densities of synaptic terminals from the two eyes (Fig. 1), arise late in development from an initially unpatterned state, through mechanisms which depend on stimulus driven and/or spontaneous nervous activity (for reviews see Kuffler, Hubel and Wiesel (1977), and also Swindale (1991)). Partly because there is a wealth of experimental data, but also because the cortical patterns are intriguing, this system has proven popular with modellers. A large (and growing) number of different models have been proposed to explain the developmental origin of the patterns. Some of the existing models are listed in Table 1. Each of these models embraces a different degree of biological realism. Some are based directly on ideas about biological mechanism in terms of the physiological factors influencing the modification of synaptic interactions. Other models use algorithms which, though biologically inspired, are by themselves non-biological. Goodhill (1992) has reviewed some of the models listed in Table 1. It is not the intention of the present paper to evaluate the relative merits of each model. Instead, the present aim is to understand some very general features shared by several of the models. Indeed, the two-dimensional spatial patterns produced by nearly every model in Table 1 are strikingly similar. The reason for this similarity of apparently distinct models has not been investigated. The issue at stake is the

question of *pattern selection*: under what conditions will a particular model or biological system produce a given two-dimensional spatial pattern? In this paper I explore the pattern selection problem in the context of a simplified model for the formation of ocular dominance stripes by deriving and then solving a set of nonlinear mode amplitude equations. This approach to spatially distributed phenomena is widespread in physics (see Eckhaus (1962), Haken (1975), but has not yet been applied to the current problem of ocular dominance stripes.

Simplified Model Equations

In this paper amplitude equations will be derived for a simplified models for ocular dominance pattern formation. The equation considered here may be derived from Swindale's (1980) equations under certain conditions, is closely related to a limiting case of the MKS model(Miller et. al. 1989), and also arises in the mean field theory of the Ising Spin Models (Tanaka, Thompson et. al., Cowan and Friedman).

Swindale's equations are given by:

$$\begin{aligned} \dot{n}_R(\vec{r},t) &\propto \int_\Omega [w_{RR}(\vec{r}-\vec{r}')n_R(\vec{r}') + w_{RL}(\vec{r}-\vec{r}')n_L(\vec{r}')]\, d\vec{r}' \\ \dot{n}_L(\vec{r},t) &\propto \int_\Omega [w_{LL}(\vec{r}-\vec{r}')n_L(\vec{r}') + w_{LR}(\vec{r}-\vec{r}')n_R(\vec{r}')]\, d\vec{r}', \end{aligned} \tag{1}$$

where n_R and n_L are densities of right and left eye synapses respectively, $\vec{r}$ is a position in a two-dimensional cortical domain Ω, and the w are intracortical interaction kernels modeling stimulatory and inhibitory effects between syanptic densities. When there is a constraint on the total density of synapses $n_R + n_L$, the model may be reduced to a single integrodifferential equation for the scalar variable:

$$a(\vec{r},t) = n_R(\vec{r},t) - n_L(\vec{r},t),$$

which is a measure of the ocular dominance as a function of position. The linear

part of the reduced system takes the form:

$$\dot{a}(\vec{r},t) \propto \int_\Omega w(\vec{r}-\vec{r}')a(\vec{r}',t)d\vec{r}'.$$

To investigate pattern selection it is necessary to introduce nonlinearity in as general a form as possible. Consider an additive nonlinearity:

$$\dot{a}(\vec{r},t) = \int_\Omega w(\vec{r}-\vec{r}')a(\vec{r}',t)d\vec{r}' + f(a). \tag{2}$$

$f(a)$ is a general nonlinear function of a which may be expanded as a Taylor series about the unpatterned state $a = 0$:

$$f(a) = \lambda a + Qa^2 + Ca^3 + \cdots$$

Alternate ways to introduce nonlinearity into (2) are under investigation. Numerical experimentation (see Fig. 2) with (2) shows that it developes qualitatively similar patterns to patterns produced by several of the models listed in Table 1.

The linear analysis of (2) is straightforward. The pattern is first written as a Fourier series with time dependent amplitudes:

$$a(\vec{r},t) = \sum_{\vec{k}} A_{\vec{k}}(t)e^{i\vec{k}\cdot\vec{r}}. \tag{3}$$

This assumes periodic boundaries but otherwise does not explicitly specify the size or shape of the domain. The analysis may be applied to other types of boundary conditions with substitution in (3) of the appropriate basis functions. The qualitative conclusions of this work are not, however, strongly dependent on the use of cyclic domains. The nature of the biologically relevant boundary condition is unknown and will not be considered further in the present paper. The linear part of (2) then becomes:

$$\dot{A}_{\vec{k}}(t) = \alpha(\vec{k})A_{\vec{k}}(t) \tag{4}$$

with:

$$W(\vec{k}) = \int_{\Omega} w(\vec{r}\,')e^{-i\vec{k}\cdot\vec{r}\,'}d\vec{r}\,' \tag{5}$$

and,

$$\alpha(\vec{k}) = \lambda + W(\vec{k}).$$

Equation (4) is an infinite set of independent linear ordinary differential equations for the $A_{\vec{k}}(t)$. The solution to the initial value problem ($a(\vec{r},t) = a(\vec{r},0)$ at $t = 0$) is then:

$$A_{\vec{k}}(t) = A_{\vec{k}}(0)e^{\alpha(\vec{k})t}.$$

The mechanism of wavelength selection by the linear part of (2) is then clear: for a local activation, lateral inhibition kernel used in such models, there is a single maximum in the Fourier spectrum (5). The eigenvalue corresponding to this fastest growing wavevector may become positive (for example as λ is gradually increased). If $w(\vec{r})$ is isotropic with respect to $\vec{r}$ then the spectrum of growth rates $W(\vec{k})$ is also isotropic in $\vec{k}$-space. Hence all modes having wavevectors on the circle $\left|\vec{k}\right| = k_{max}$ will have the same (maximum) growth rate. After a short time the pattern is characterized by a single wavelength.

Nonlinear Mode Amplitude Equations

To analyse the behaviour of the nonlinear system (2), the solution is again written as a Fourier series. Inserting (3) into (2) and isolating individual mode amplitudes by Fourier transformation leads to the following infinite set of coupled nonlinear ordinary differential equations for the mode amplitudes:

$$\dot{A}_{\vec{k}}(t) = \alpha(k)A_{\vec{k}} + Q\sum_{\vec{k}'\vec{k}''} A_{\vec{k}'}A_{\vec{k}''}\delta_{\vec{k},\vec{k}'+\vec{k}''} + C\sum_{\vec{k}'\vec{k}''\vec{k}'''} A_{\vec{k}'}A_{\vec{k}''}A_{\vec{k}'''}\delta_{\vec{k},\vec{k}'+\vec{k}''+\vec{k}'''} \tag{6}$$

$f(a)$ has been Taylor expanded about the unpatterned state $a = 0$ to third order in a. Though the presence of the Kronecker deltas in the double and

triple sums over wavevectors reduce the number of mode couplings, (6) is too complicated to be solved exactly. Approximate solutions may be obtained in the region of parameter space close to the onset of the pattern forming instability. Specifically, the linear parameters λ and $w(\vec{r})$ may be adjusted so that:

$$\begin{aligned} \alpha(k_c) &> 0 \\ \alpha(k) &< 0 \quad k \neq k_c \\ \alpha(k) &\gg \alpha(k_c). \end{aligned} \tag{7}$$

Then the adiabatic (or quasi-steady state) approximation:

$$\dot{A}_{\vec{k}} \approx 0 \quad k \neq k_c \tag{8}$$

may be used to eliminate from (6) the dynamics of all modes but the unstable ones ($k = k_c$). Intuitively, conditions (7) ensure that the dynamics of the stable modes is much faster than the dynamics of the unstable modes, whence the the amplitudes of the stable modes rapidly adapt to the current amplitudes of the unstable ones. Equations (8) supply a set of coupled nonlinear algebraic equations relating the stable and unstable mode amplitudes. These are used to eliminate the stable mode amplitudes from (6) leaving a self-contained, finite set of nonlinear mode amplitude equations for the unstable (or pattern forming) modes. Analysis of the steady states and stability of the mode amplitude equations provide insight into nonlinear pattern selection. Several relevant examples of this calculation will now be discussed.

The simplest example is the one dimensional cyclic domain. To derive the amplitude equations to third order in A_{k_c} note that A_0 and A_{2k_c} have second order terms:

$$\begin{aligned} A_0 &\approx \frac{-2Q}{\alpha(0)} A^*_{k_c} A_{k_c} \\ A_{2k_c} &\approx \frac{-Q}{\alpha(2k_c)} A^2_{k_c} \end{aligned} \tag{9}$$

(* denotes complex conjugate). Then the critical mode amplitude equation to third order in A_{k_c} is:

$$\dot{A}_{k_c} = \alpha(k_c) A_{k_c} + c_s \left|A_{k_c}\right|^2 A_{k_c} \tag{10}$$

with:

$$c_s = \left[3C - \frac{4Q^2}{\alpha(0)} - \frac{2Q^2}{\alpha(2k_c)}\right]$$

The steady state mode amplitudes may be calculated from $\dot{A}_{k_c} = 0$, and the stability of these solutions depends on the sign of the derivative $\partial \dot{A}_{k_c}/\partial A_{k_c}$. There are two solutions which exchange stability as $\alpha(k_c)$ changes sign:

$$\begin{aligned} \text{(i)} A_{k_c} = 0 \quad & \text{stable for } \alpha(k_c) < 0 \\ \text{(ii)} \left|A_{k_c}\right|^2 = \frac{-\alpha(k_c)}{c_s} \quad & \text{stable for } \alpha(k_c) > 0 \end{aligned}$$

The time dependent solution to (10) is:

$$\begin{aligned} A_{k_c}^2(t) &= \frac{\alpha(k_c) e^{2\alpha(k_c)t}}{c_s e^{2\alpha(k_c)t} + \alpha(k_c) D} \\ D &= \frac{1}{\alpha(k_c)} \left[\frac{\alpha(k_c)}{A^2(0)} + c_s\right]. \end{aligned} \tag{11}$$

Numerical solution of (2) compares favourably with (11) (see Fig. -), providing a check of the validity of the adiabatic approximation for analysis of (2).

The situation for a two-dimensional domain is more complicated as several spatial modes with differently oriented wavevectors may share the same growth rate. The problem is simplified considerably for nonlinear functions which lack quadratic terms in their Taylor expansion ($Q = 0$). In this case there are no direct couplings of the critical modes with stable modes with order less than fifth in A_{k_c}. Hence the mode amplitude equations for an arbitrary number N of modes with $\left|\vec{k}\right| = k_c$ are :

$$\begin{aligned} \dot{A}_i = \alpha A_i + (c_s \left|A_i\right|^2 + c_0 \sum_{j \neq i} \left|A_j\right|^2) A_i, \quad i = 1 \cdots N \\ c_s = 3C \quad c_o = 6C \end{aligned} \tag{12}$$

where the subscript k_c has been dropped for brevity of notation. Equation (12) has a family of solutions parametrized by the number of non-zero amplitudes M, given by:

$$A_i^2 = \frac{-\alpha}{c_s + (M-1)c_0},$$

the amplitudes of the remaining $N - M$ modes are zero. To examine the stability of these solutions the eigenvalues of the Jacobian $\partial \dot{A}_i / \partial A_j$ are calculated. It is found that solutions with $M > 1$ are always unstable, while the $M = 1$ solutions, corresponding to stripes at a particular orientation, are stable provided $\alpha > 0$. With $\alpha < 0$ only the unpatterned state is stable.

Now consider the situation where $Q \neq 0$, but the boundary conditions (*i.e.* shape of the domain) are such that $\delta_{\vec{k},\vec{k}'+\vec{k}''} = 1$ cannot be satisfied for any three modes. Then there are no direct quadratic couplings of unstable modes, however indirect couplings via the zeroeth and second harmonics contribute to third order terms in the amplitude equations:

$$\dot{A}_i = \alpha A_i + (c_s A_i^* A_i + \sum_{j \neq i} c_{ij} A_j^* A_j) A_i \tag{13}$$

with,

$$c_s = 3C + \frac{4Q^2}{\alpha_0} + \frac{2Q^2}{\alpha_2} \tag{14}$$

$$c_o = 6C + \frac{4Q^2}{\alpha_0} + \frac{8Q^2}{\alpha_2} \tag{15}$$

and,

$$\alpha_0 = \alpha_{0\vec{k}_c} \quad \alpha_2 = \alpha_{2\vec{k}_c} \quad \alpha_{i+j} = \alpha_{\vec{k}_i + \vec{k}_j}$$

In principle, (13) may be solved in an analogous manner to 12, that is as a set of linear algebraic equations for the $A_i^* A_i$. However, c_{ij} is now angle-dependent, requiring solution of these equations in a case by case fashion. The simplest example is a square domain with wavenumber chosen so that plane waves in two perpendicular directions fit the boundaries. The the amplitude equations

are:

$$\dot{A}_a = \alpha A_a + (c_s A_a^* A_a + c_o A_b^* A_b) A_a \quad (16)$$

$$\dot{A}_b = \alpha A_b + (c_o A_a^* A_a + c_s A_b^* A_b) A_b \quad (17)$$

with c_o, c_s given above. The three classes of solution are:

- homogeneous $A_a = A_b = 0$ stable for $\alpha < 0$
- stripes $|A_a| = \sqrt{\frac{\alpha}{c_s}}$, $A_b = 0$ and vice-versa stability condition
- square spots $|A_a| = |A_b| = \sqrt{\frac{alpha}{c_s + c_o}}$

Solutions II and III are stable for mutually exclusive values c_s, c_o (or, equivalently Q, C). Furthermore, $Q = 0$ corresponds to parameters satifying conditions for solutions II to be stable. Small perturbations of a quadratic nonlinearity do not destabilize the striped solutions.

Finally, suppose $Q \neq 0$ and $\delta_{\vec{k},\vec{k}'+\vec{k}''} = 1$ is permitted for some of the available modes. A case by case analysis of particular boundary conditions is again needed. Moreover, the fixed point equations are no longer linear in $A_i^* A_i$ so that analysis becomes more complicated. We have obtained the solution for six unstable modes oriented such that the $\vec{k}$ are at the vertices of a hexagon in k-space. The three mode amplitude equations are then:

$$\dot{A}_a = \alpha A_a + 2Q A_b^* A_c + (c_s A_a^* A_a + c_o (A_b^* A_b + A_c^* A_c) A_a \quad (18)$$

$$\dot{A}_b = \alpha A_b + 2Q A_c^* A_a + (c_s A_b^* A_b + c_o (A_a^* A_a + A_c^* A_c) A_b \quad (19)$$

$$\dot{A}_c = \alpha A_c + 2Q A_a^* A_b + (c_s A_c^* A_c + c_o (A_b^* A_b + A_a^* A_a) A_c \quad (20)$$

Salient features of the analysis: both striped and spotted solutions are possible. However, now region of stability is not mutually exclusive. Stability conditions indicate that the region of stability of the hexagonal spotted solution decreases as $|Q|$ is decreased.

Discussion

The two dimensional spatial patterns of several models for ocular dominance column development show strong similarities. Where similar behaviour is observed one should ask whether there are unifying principles underlying the similarities, or if the agreement is a coincidence. While most of the proposed models faithfully reproduce experimental data, none has satisfactorily explored the question of nonlinear pattern selection. The problem requires an understanding of the nonlinear behaviour of a given model and is best tackled first on a simplified system.

Several of the models mentioned here use similar dynamical systems to produce spatial pattern (specifically the integrodifferential equation models (Swindale 1980; Miller, Keller and Stryker, 1989), the Ising spin models (Tanaka; Thompson et. al.; Friedman and Cowan), and the bandpass filtered spatial noise algorithm (Rojet and Schwartz, 1990). In terms of their linear properties, these models make use of an intracortical interaction function with local activation and lateral inhibition, corresponding to a bandpass filtering for spatial frequency. This explains wavelength selection but not selection of a particular two dimensional pattern. All of the models investigated treat left and right eye synaptic terminals to the cortex of either hemisphere equally (when modelling the normal pattern of ocular dominance). In the simplified system (2) analyzed here, this implies that the quadratic term in $f(a)$ vanishes. The relation between the strength of the quadratic nonlinearity and stripe selection established in this work thus provides a rationale for the similarities in the behaviour of disparate models. This principle may apply to biological systems as well. In the macaque monkey, approximately equal numbers of axons innervate the primary visual cortex of each hemisphere. A pattern of well defined, branching stripes (Fig. 1 (a)) is observed. In the cat, where there is a greater number

of synapses from the contralateral (opposite) eye, the pattern is splotchy (Fig. 1(b)). It would be interesting to investigate whether a correlation between spatial pattern of ocular dominance and a symmetry between numbers of afferents from the two eyes, holds for other species. In the frog *Rana pipiens*, ocular dominance patterns may be artificially induced by surgical implantation of a third eye, which causes two of the eyes to project to the optic tectum (for a review of the experimental results on 3-eyed frogs see Fraser and Perkel, 1990). One would guess that the transplanted eye and the native one would project approximately equal numbers of axons to the tectum. In fact a striped pattern, not unlike the monkey stripes, is observed. A further test of the principle would be to reduce the number of axons projecting from the transplanted eye before implantation and observe the effect of such perturbations on the ocular domininance pattern in the tectum.

It is worth noting that the simple integrodifferential equation model studied in this paper (as well as several other models mentioned above) share features with Turing reaction-diffusion systems. An application of the mode amplitude analysis technique used here has been previously applied to stripe selection in Turing systems (Lyons and Harrison, 1991). Independently, Ermentrout (1991) used bifurcation theory to derive pattern selection rules for reaction-diffusion systems on the unit square. After the completion of this work, S. Tanaka has informed me that he has recently performed an analysis of pattern selection by his model using a related but distinct approach (Tanaka, 1993).

Acknowledgements

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Table 1 Selected models for ocular dominance column development

Author(s)	Mechanism/Algorithm
von der Malsburg (1979)	Chemical Markers
Swindale (1980)	Intracortical Interaction
Miller Keller and Stryker (1989)	Correlation-based
	+ Intracortical Interaction
Fraser and Perkel (1990)	Multiple Constraints
Goodhill and Willshaw (1990)	Elastic Network
Tanaka (1990)	Ising Spin System
Thomson et. al. (1990)	Ising Spin System
Rojet and Schwartz (1990)	Bandpass Filtered Spatial Noise
Cowan and Friedman (1991)	Ising Spin System
Obermeyer Ritter and Schulten (1991)	Self Organizing Feature Map
Jones Van Sluyters and Murphy (1991)	Optimal Spatial Map

Figure Legends

Fig. 1. Patterns of ocular dominance generated by various existing developmental models. From left to right, top to bottom: elastic net algorithm (Goodhill and Willshaw); Ising spin model (Tanaka); optimal spatial map (Jones et. al.); intracortical interaction (Swindale).

Fig. 2. Patterns of ocular dominance in the primary visual cortex of macaque monkey, **a**, and cat, **b**. In both cases bright regions indicate a predominance of input to the cortex from the ipsilateral eye. Adapted from digitally scanned images of **a**, figure 5 of (Levay et. al. 1980) and **b**, figure 7b of (Anderson et. al. 1988).

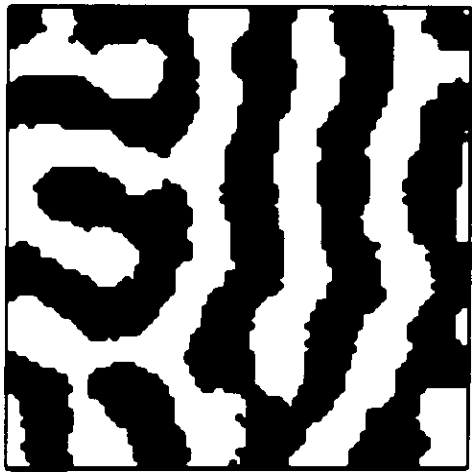
Fig. 3. Time evolution of the ocular dominance, $a(\vec{r}, t)$,, according to equation - (see text), starting from spatial random noise. **a** $t = 0$, **b** $t = 5$, **c** t=10 ,**d** $t = 500$. The domain is a 128×128 square grid of cells with periodic boundary

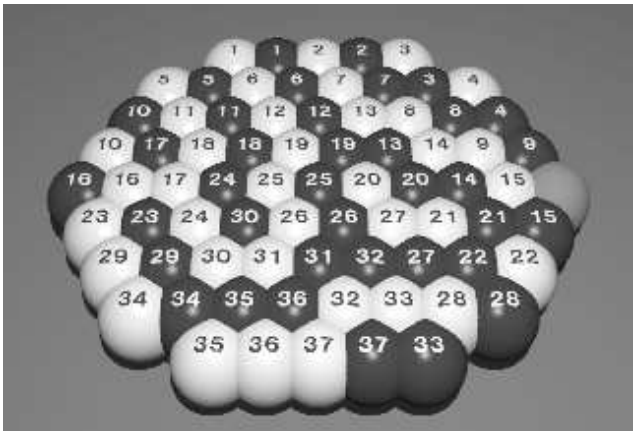
conditions. Parameters for this run: $\beta = 0.2, x_\beta = 5, \gamma = 0.1, x_\gamma = 20, \lambda = -1.0, Q = 0.0, C = -1.0$. The timestep for the numerical integration was 0.05. The initial values of a at each cell of the grid were independently chosen from a uniform distribution on (,). Equation - was solved numerically using a second order Runge-Kutta method, with the convolution integral evaluated in the fourier domain.

Fig. 4. Critical mode amplitude A_{k_c} as the eigenvalue $\alpha(k_c)$ is increased. The data points were obtained by numerical solution of - on a one dimensional cyclic domain. The curves are approximate analytical predictions, -. Linear parameters for these runs are $\beta = 0.2, x_\beta = 80, \gamma = 0.1, x_\gamma = 320$. The coefficients of the nonlinear terms are given in the figure. With this choice of parameters the critical mode has a wavelength approximately equal to a third of the length of the domain.

Fig. 5. Time evolution of the critical mode amplitude, A_{k_c}, and its third harmonic, A_{3k_c} (shown magnified $10\times$). Data points were obtained by numerical solution of -, curves by the approximate analytical results -. Parameters for this run were: $\beta = 0.2, x_\beta = 80, \gamma = 0.1, x_\gamma = 320, \lambda = -1.4, Q = 0.0, C = -0.2$.

Fig. 6. Spatial pattern of ocular dominance (at $t = 50$) as the magnitude of the quadratic nonlinearity is increased. **a** $Q = 0.1$, **b** $Q = 0.3$,**c** $Q = 0.6$. All other parameters and the initial state are the same as for fig. 2.

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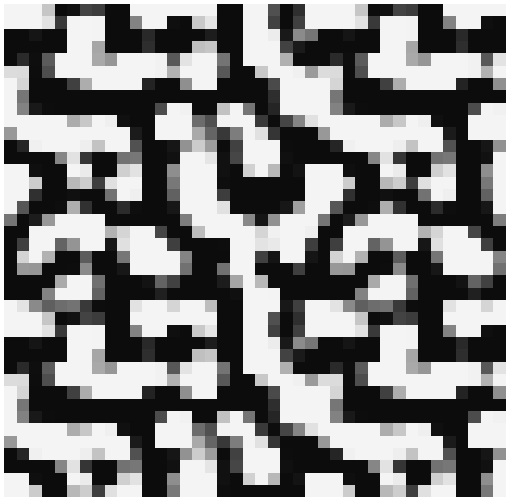

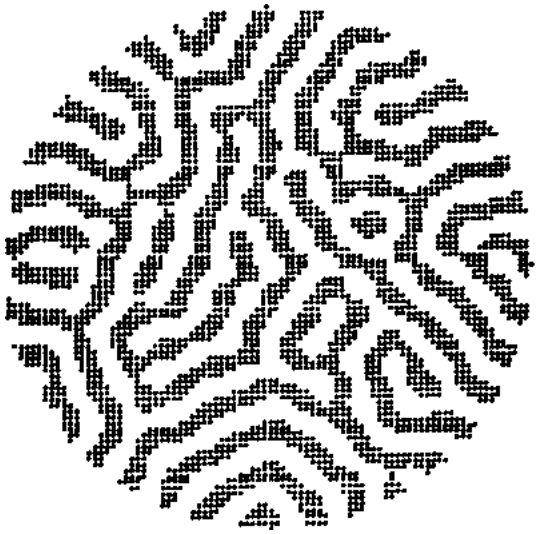

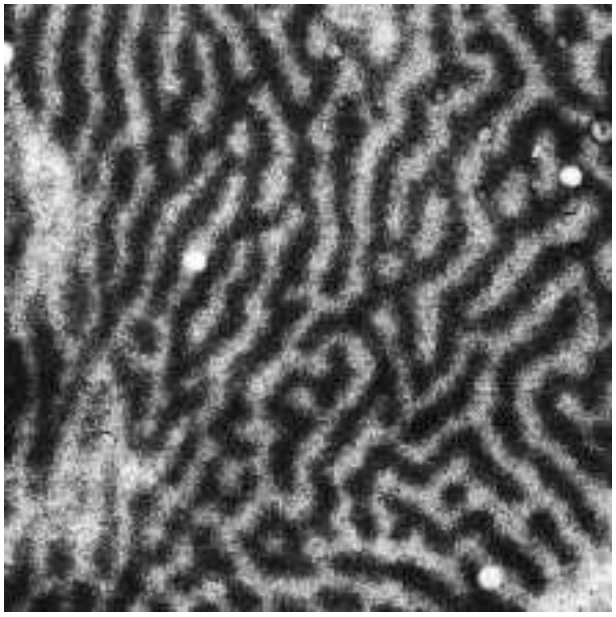

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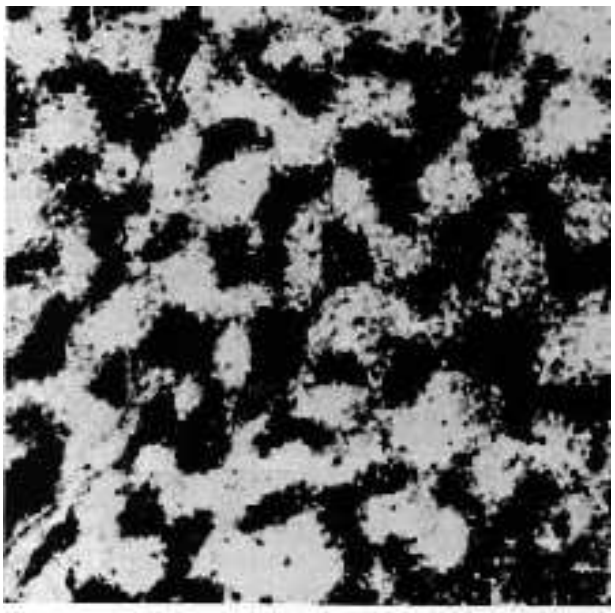

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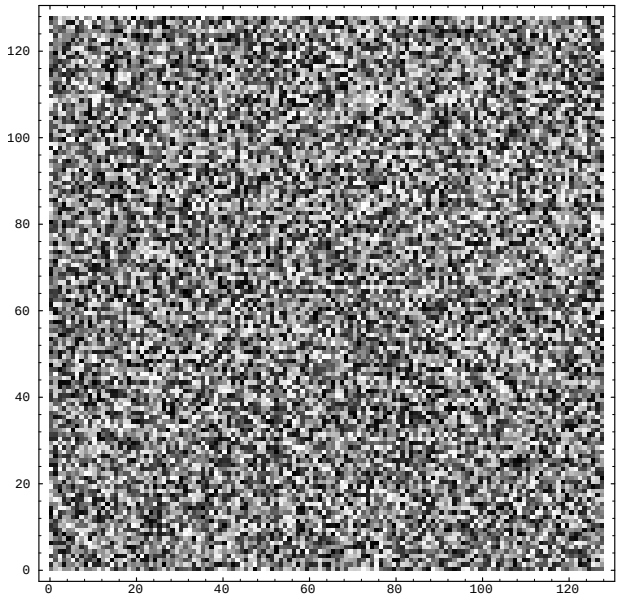
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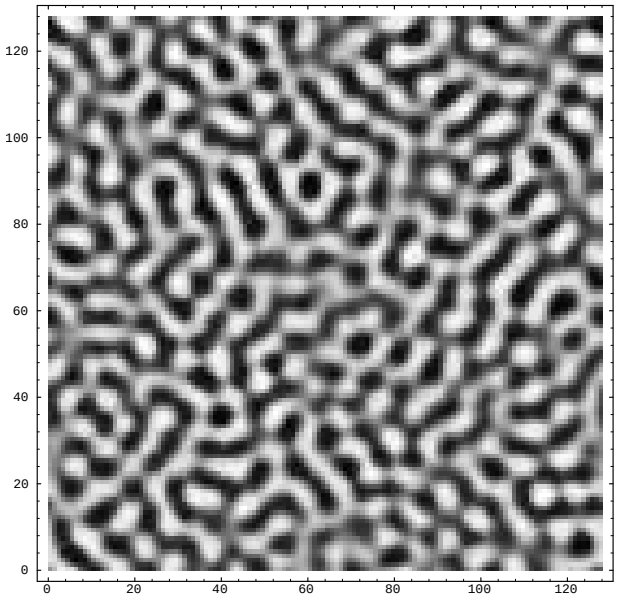
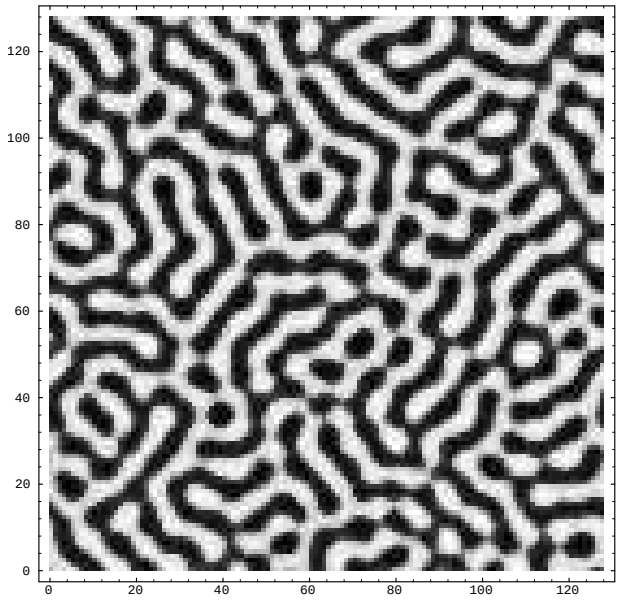
40
60
80
100
120

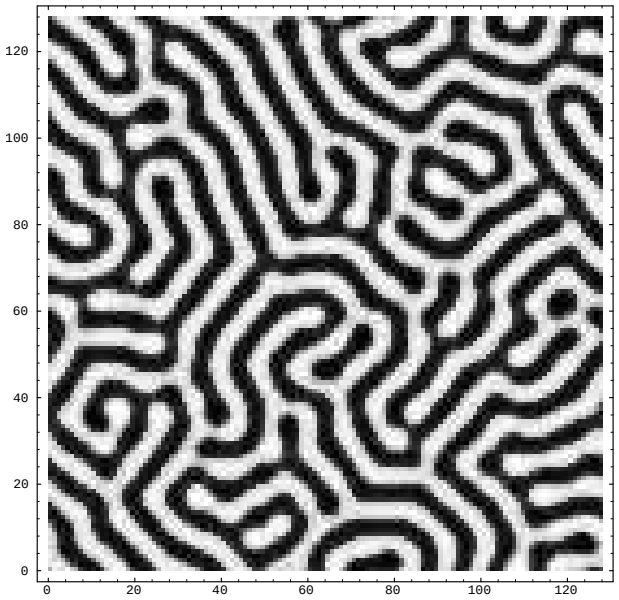
a


0
20
40
60
80
100
120

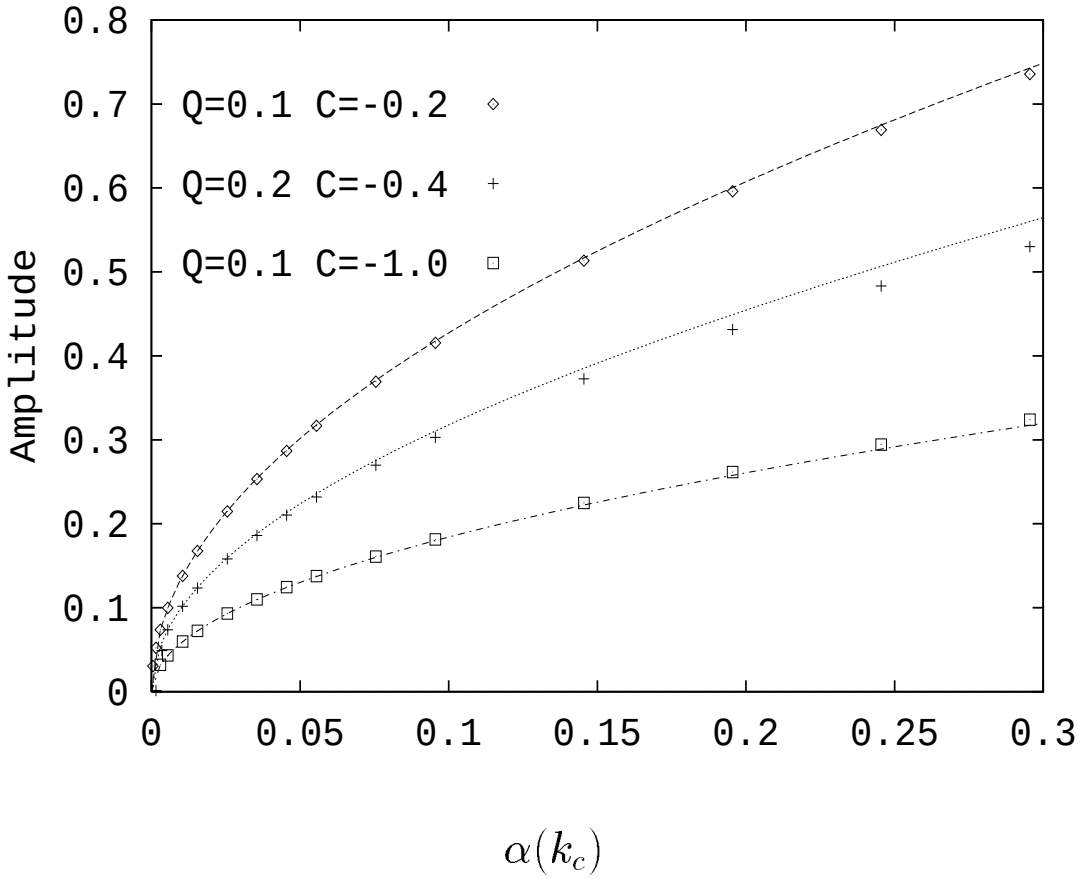
b

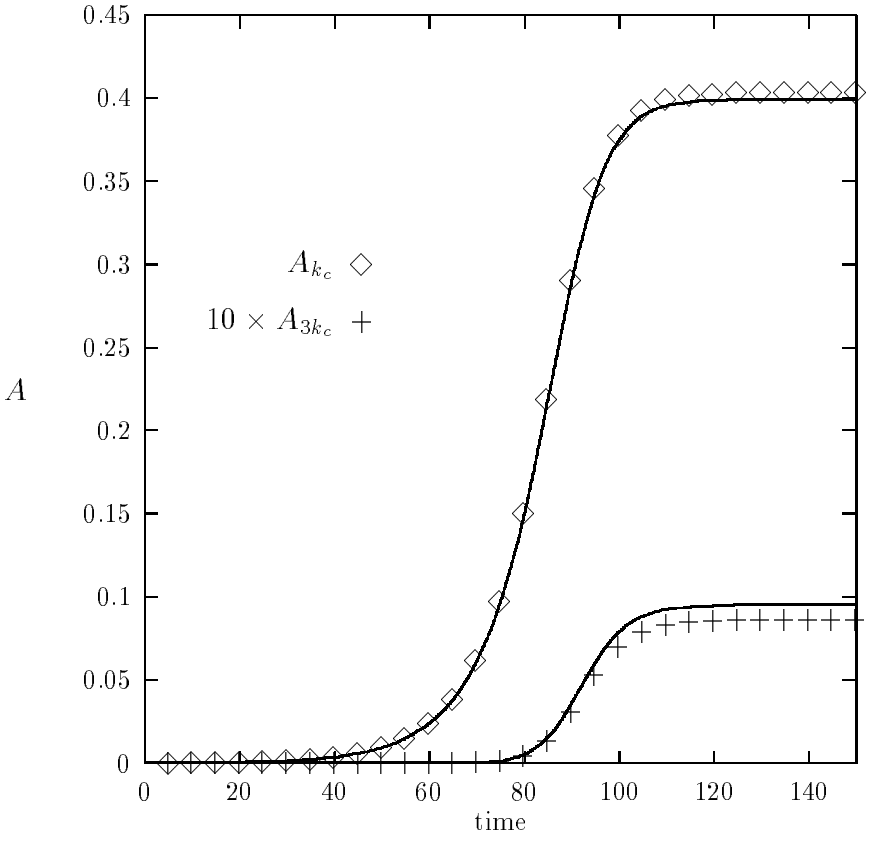

0
20
40
60
80
100
120

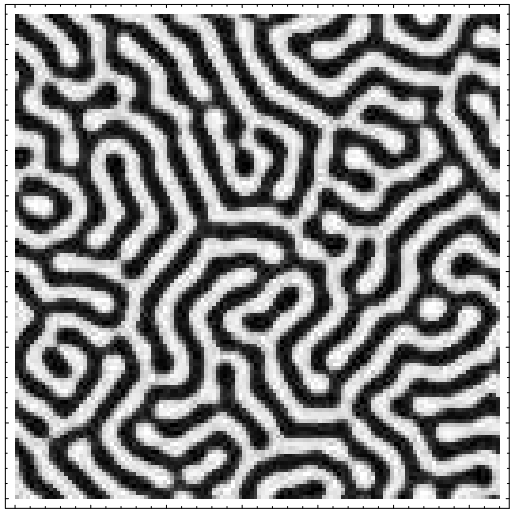
c


0
20
40
60
80
100
120

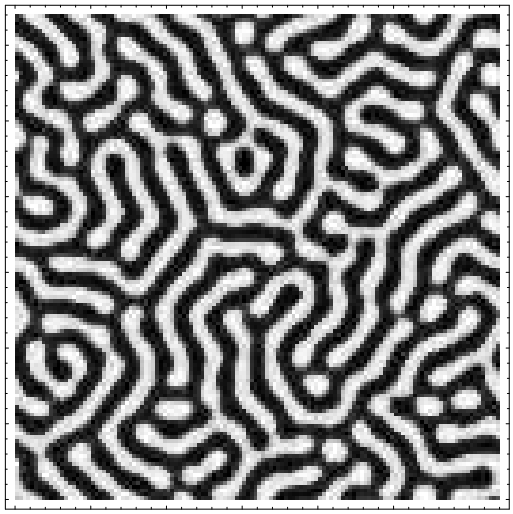
d


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Amplitude
Q=0.1 C=-0.2
Q=0.2 C=-0.4
Q=0.1 C=-1.0
0
0.05
0.1
0.15
0.2
0.25
0.3
$\alpha(k_c)$

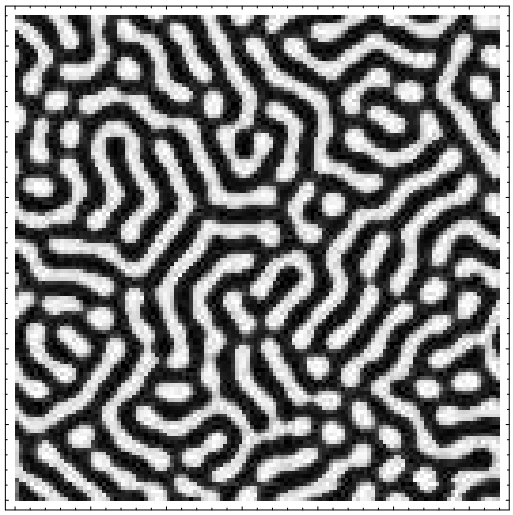

0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
A
A_{k_c} ◇
$10 \times A_{3k_c}$ +
0
20
40
60
80
100
120
140
time



a



b



c

ARCHIVAL NOTE

Added in 2026; not part of the original manuscript.

Pattern selection in models of ocular dominance column development is an unpublished manuscript by Michael J. Lyons, written while the author was a Research Fellow in Computation and Neural Systems at the California Institute of Technology.

The surviving source files record development of the manuscript from February through June 1993. The original title source specifies `\date{\today}` rather than a fixed date. The date **June 1993** displayed in the reconstructed PDF was inferred from the surviving source chronology, which extends through 10 June 1993.

This PDF was reconstructed in 2026 from surviving TeX, PostScript, and related source files. The manuscript has not been revised to incorporate later research or to complete unfinished arguments. The six surviving figures were appended as separate pages following the manuscript text.

The manuscript remains unfinished. It contains unfilled equation and figure cross-references, typographical errors, and an unresolved sign inconsistency in the amplitude coefficients for non-zero Q in the section "Nonlinear Mode Amplitude Equations" (equations 14-15 compared with equation 10). This does not affect the separately derived $Q = 0$ stripe-selection result. Figure 1 contains five panels, while the surviving caption identifies only four models; no attempt has been made to determine or supply the missing identification. No attempt has been made to correct these matters in the archival reconstruction.

The complete archival deposit includes the surviving manuscript source archive, original figure material, and a detailed README.txt documenting provenance, source dates, figure-file correspondence, reconstruction, and known unresolved items.

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